THE GROWTH AND REGENERATION OF THE GILLS IN THE YOUNG NECTURUS.

ALBERT C. EYCLESHYMER,

DEPARTMENT OF ANATOMY, ST. LOUIS UNIVERSITY, ST. LOUIS, MO.

During the summer of 1904 the writer made a series of observations and experiments on the growth and regeneration of the gills of the larval *Necturus*. The work was done with the hope of obtaining more information as to the relation which the regenerated gill bears to the normal in its rate of growth, in its size, and particularly in its pattern.

The larvæ were kept in aquaria, from which they were taken at intervals, placed in flat-bottomed watch-glasses above mirrors, and sketches made of the ventral surfaces of the gills. The period of observation on the growth of the normal gills was from the time (12–13 mm) of their first appearance, to the time (18–20 mm.) when four pairs of filaments were present. At this time the gills were cut off and preserved.

These larvæ were then placed in separate aquaria and like the normal were sketched at successive intervals. The period of observation on the regenerating gills was from the time of excision until about the same number of filaments were present as in the normal at the time when they were cut off.

Ten series were started, but only eight were completed, owing to the death of two larvæ. That the normal processes might be as little disturbed as possible but a single gill was removed from each larva. This one was in each case the anterior on the right side of the head. Since the eight experiments gave similar results, but three have been described and illustrated in detail.

The first appearance of the gill bars is to be seen in the 9–10 mm. larva as slight swellings on each of the three gill arches. When the larva has reached a length of 12–13 mm., the first and second gill bars measure about 1.0 mm., while the third measures 0.5 mm.

The first gill filament appears at this time as a slight swelling

on the postero-ventral surface of the first bar, midway between its base and apex; soon a second filament appears on the antero-

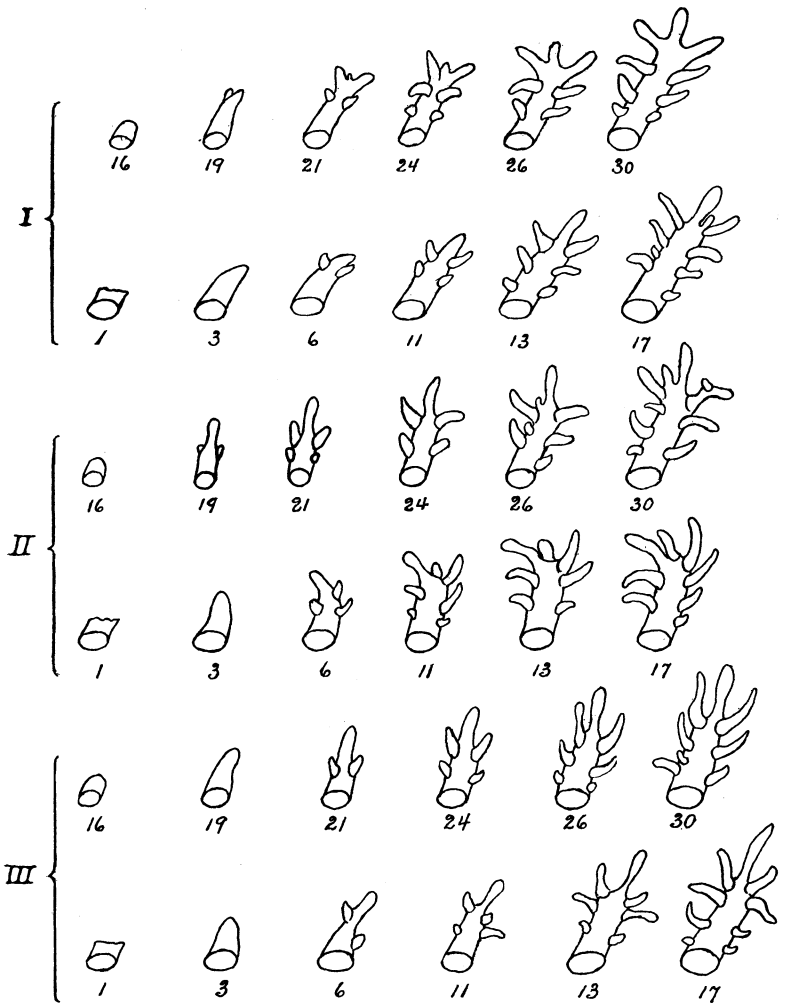

FIG. 1. Each series is bracketed and designated by Roman numerals. The upper row in each series represents the changes in the normal gill. The lower row of each series represents the changes in the regenerating gill of the same larva. The numerals indicate the days of the month: June 16–30 and July 1–17. All the figures are magnified about ten times.

ventral surface opposite the first, as shown in Ser. II., Fig. 19. Often the buds form at different levels, giving rise to unsymmet-

rical patterns. While the lateral buds are elongating the tip of the gill bar becomes drawn out into a median filament, as in Ser. III., Fig. 21. Sometimes the tip of the gill bar forms one of the first pair of filaments, in which case a median bud forms the median or apical filament.

A second pair of filaments forms some 48 to 60 hours later. In most cases these are bilaterally symmetrical, as indicated in Fig. 21. In two out of the eight series the buds did not arise at opposite points, and in these cases more or less irregularity occurred in the succeeding pairs.

The third pair of filaments shows considerable variation both in time and place of origin. In five cases they appeared about 48 hours after the second pair. In the remaining three cases they were not formed until the end of the third day. The filaments of this pair usually arise in such positions that they are bilaterally symmetrical, as shown in Ser. III., Fig. 26. In two series conditions were observed something like that represented in Ser. II., Fig. 26, where only one of the third pair arose in the usual position. In place of the other there arose an intercalated bud on the opposite side.

The fourth pair of filaments may develop as bilaterally symmetrical structures, as in Ser. I., Fig. 30, or may be represented by a single intercalated filament, as in Ser. III., Fig. 30, or again the filaments may show such great irregularity that it is impossible to tell what filaments are to be considered as belonging to the fourth pair, as in Ser. II., Fig. 30.

In the later growth of the gill the filaments not only continue to form in pairs at the base of the gill bar but also to arise irregularly from intercalated buds. In addition the filaments send off lateral branches which form secondary filaments. In the older larvæ (30–40 mm.) the patterns become more and more irregular.

As a general statement one might say that in the earliest filaments much regularity prevails, but in the formation of the later filaments the regularity decreases.

When the gills had reached the stages shown in Fig. 30 they were cut off with spring scissors as near the head as possible and as they regenerated their changes were carefully followed and

compared with the successive changes observed in the growth of the normal gills.

In Ser. I. the first pair of buds formed at about the same relative time as in the normal, but instead of conforming to the rather exceptional pattern of the normal they were symmetrically placed, as shown in Fig. 6. The second pair of filaments while symmetrical were not present until 96 hours later. In the normal the second pair arose 72 hours after the first pair. The third pair appeared some 48 hours after the second and in both time and place of origin conformed to the normal. The condition about 132 hours later is shown by Fig. 17. Comparing this figure with Fig. 30 it will be noted that but a single filament is present to represent the fourth pair of the normal. Again there are present two intercalated buds while the normal shows none.

In Ser. II. the filaments appear later than in the normal and instead of arising as a pair there are three buds present (Fig. 6). As the later stages show, the first pair is made up by the tip of the median and the first lateral filament. About 96 hours later, as shown in Fig. 11, three more buds are present. Two of these form a new pair at the base of the gill bar, while the third arises between the tip of the gill bar and the first lateral filament. When compared with the normal of this stage it is obvious at a glance that there is no conformity. No other changes occur which merit detailed description. If the stage shown in Fig. 17 be compared with that of the normal shown in Fig. 30 it will be readily observed that the regenerated gill is quite unlike the normal, but on the whole it presents a more regular pattern than the normal.

In Ser. III. the first pair of filaments appeared at about the same relative time as in the normal but at widely separated points, as shown in Fig. 6. The second pair formed some 96 hours later and, alternating with those of the first, gave rise to the pattern shown in Fig. 11. The third pair, as shown in Fig. 13, appeared 72 hours after the second as symmetrically placed structures. The fourth pair were likewise symmetrically placed.

It may be remarked that the remaining five series showed, with slight variations, the same results as described above. In the entire eight series not a single case was observed in which the

pattern of the growth changes in the normal gill were repeated in the regenerating gill.

If we compare the rate of growth in the regenerating gill with the rate of the normal gill we find that the stage reached in normal growth in sixteen days is reached in regeneration in about eighteen days.

That the pattern of the growing gill is not retraced by the regenerating has been established beyond question in these experiments. In the regeneration of the foot of the young *Necturus* the course of normal development is pretty accurately repeated and the same is known to be true of many other forms.

Previous experiments by others seem to indicate that if wide variations occur in normal growth we should expect to find like wide variations in regeneration.

One pattern of gill is as efficient for respiration as another provided it posesses the same number of filaments. The same is true of the regenerated gill. The normal pattern of the foot is duplicated in regeneration because the type evolved is that best adapted to the needs of the animal.

If these considerations be well founded we are led to regard physiological efficiency as the important factor in the regeneration of the gills.

In other words we may conclude that functional and structural regeneration may run parallel or they may follow widely diverging lines.